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IMMATURE SPECIMENS OF PENELLA FILOSA.

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The young stages of all parasitic Crustacea are of interest, and this is especially true with respect to the highly modified forms. Hence I was pleased to find among a number of *Penella filosa* loaned me by Dr. J. S. Kingsley, a few immature specimens. *Penella filosa* is the commonest species of *Penella* on our coast and in all probability is unhesitatingly to be identified with the form described from the sword-fish by Linnaeus in 1758 as *Pennatula filosa* under the impression that it was a Sea Pen, an error first corrected by Pallas eight years later. This species infests the sun-fish — *Orthogoriscus* — as well as the sword-fish — *Xiphias* — and the double host has suggested to some investigators that the name "filosa" covered an assemblage of ill-described *Penellas* rather than characterizing a distinct species. This view, however, does not seem well taken. With respect to the forms usually called by the name "filosa," material from either the sun-fish or the sword-fish presents no constant peculiarities by which the source may be determined. My immature specimens were taken from sword-fish.

The adult *Penella filosa* frequently attains a length of 130 mm. and may be over 20 cm. long. Of this, almost one half, the round "head" and slender cylindrical "præ-thorax," is buried in the tissues of the host. Only the thicker "post-thorax" and brush-like abdomen trail free in the sea-water, furnishing a locus for a dense growth of hydroids and occasionally barnacles, *Conchoderma*. The abdomen is less than one third of the exposed part of the animal and owes its brush-like appearance to from twenty to thirty pairs of lateral appendages each of which is subdivided into numerous thread-like branches. The trailing egg-sacs are filiform and not infrequently measure 8 or 10 cm. in length. The "head" retains minute, elongate, first, and stouter, chelate, second antennæ on the dorsal surface. Mouth parts are absent and the ventral and anterior surfaces of the "head"

are tuberculated. Behind the "head" the præthorax bears four pairs of minute limbs and forward from the anterior pair of these a stout, blunt "horn" projects on either side. This arrangement of horns, however, is not invariable and out of thirty specimens at my disposal from *Orthagoriscus mola* I found nine with an additional dorsal horn. A similar variation in the number of the horns was noted in *Penella varians* by its describers (Steenstrup & Lütken, '61) and parallel conditions are frequently met among parasitic Copepoda which attach to their hosts by analogous structures. A typical specimen of the Lernæenicus of the Menhaden for example — *L. radiatus* — has five simple horns; but specimens are commonly taken which possess a greater or lesser number of these *haftorgane* and not infrequently they are forked or are rough with small branches.

The immature *Penella* in the collection loaned me were five in number. To these a young *Penella filosa* taken from a swordfish brought into Woods Hole has been added, so that my series included six specimens. The youngest individual (*A*) (Fig. 1), had a distinct cylindrical cephalothorax, highly convex, with a double-lensed median eye near the anterior end. Beyond the border of the cephalothorax the three-jointed (?), hamate second antennæ projected. This cephalothorax was flecked with considerable black pigment. The filiform thorax extended to a length thirty-two times that of the cephalothorax. It was not segmented but ringed as in the adult with indistinct circular constrictions near the hinder end. The abdomen was filiform, bore along its sides twenty-two pairs of short unbranched lateral appendages and terminated with a deep notch. On either side of this was a small bisetose appendage. The first pair of antennæ were delicate, two-jointed, and setose. A prominent, urn-shaped rostrum with a reflected, finely serrate border projected from the venter of the cephalothorax and was flanked by reduced maxillæ in the form of minute palps each tipped with two delicate bristles. No traces of mandibles were found. Just behind the rostrum in the mid-line there was a prominent rounded tubercle and on either side of this the two-jointed maxillipeds were situated. Further back, two shallow depressions and back of these two larger shallow pits were visible.

The thoracic limbs appeared to be much like those of an adult *P. filosa* as far as it was possible to examine them. No traces of appendages other than these just mentioned were found. This

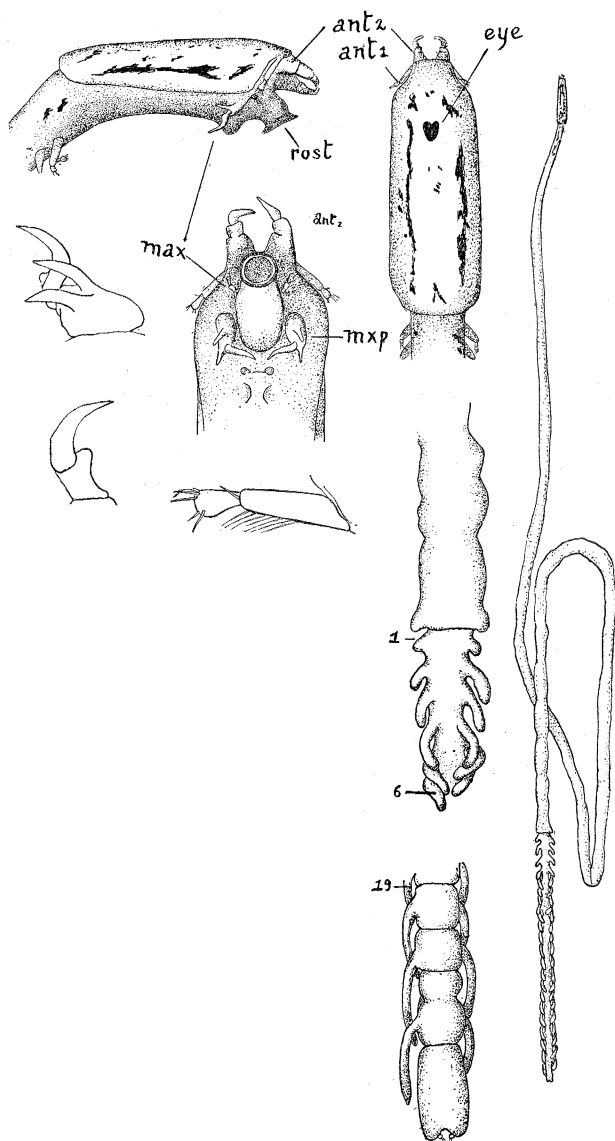


FIG. 1. Youngest larva of *P. filosa*; with three aspects of the carapace, anterior and posterior extremities of the abdomen, maxilliped, first and second antennæ more enlarged.

specimen was 94 mm. long; of which the head measured 2.5 mm., the thorax 80 mm., and the abdomen 11.5 mm.

The next older specimen (*B*) shows a marked advance in development over "*A*" (Fig. 2). The cephalothorax and thorax are no longer distinctly demarked from one another and the sides of the anterior portion of the former region are inflated so that a "head" is differentiated. On the dorsal surface, in the neighborhood of the antennæ, a trace of the borders of the cephalo-thorax still persist. In the region of the anterior pair of thoracic limbs, behind the newly-formed "head" a pair of blunt horns have made their appearance. The median eye was not noted in this individual. The antennæ and maxillipeds are much the same as in stage "*A*," except that the second antennæ are now more chelate. The rostrum is distinctly shifted toward the anterior border of the head and the median tubercle is now reinforced by a conical tubercle on either side of the rostrum. Whether this pair of tubercles replace the maxillæ or not is uncertain. These appendages were not observed in the specimen under consideration, but the minute palps to which they are reduced were doubtfully traced in the next older specimen mesad from the lateral tubercles. The abdominal appendages are uniramous as before. The length of "*B*" was 130.5 mm. The "head" measured 2.5 mm. long by 1.2 mm. wide, the thorax was 120 mm. long, the abdomen 8 mm. long.

The third specimen (*C*) differed from "*B*" in the still more inflated "head" and in the replacement of the maxillipeds by a pair of tubercles, so that the ventro-anterior face of the "head" now presented five tubercles, one median and four paired. The rostrum of this stage pointed in a line with the axis of the "head" and its tip together with the tips of the anterior pair of lateral tubercles were visible from above. The dimensions of

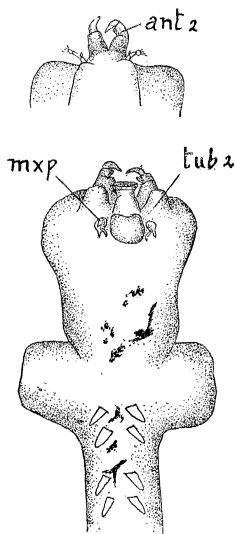


FIG. 2. Second oldest larva "*B*" of *P. filosa*; dorsal and ventral aspects of the head.

"C" were; head 2.5 mm., thorax 132 mm., abdomen 12 mm. The "head" was 1.8 mm. broad at the widest; the horns spread 2 mm.

In the fourth member of my series "D" (Fig. 3) the chief change is the further progress of the shifting upward of the anterior face of the "head." The tips of the rostrum and anteriormost tubercles are visible from above as before. The antennæ have migrated to the upper surface of the "head" and the apices of the second pair are distant from the anterior border. These antennæ are adult in form. A few of the abdominal appendages consisted of a main ramus and two minute accessory rami, but the majority of this series of appendages had only a single accessory branch and the first five or six pairs were uniramous. The "head" of

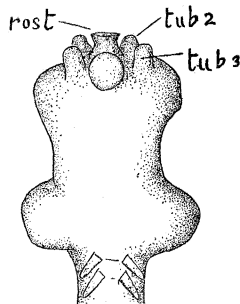


FIG. 3. Fourth larva "D" of *P. filosa*; ventral aspect of the head.

this specimen measured 3.5 mm., the body 130 mm., the abdomen, 16.5 mm.

Of the two remaining specimens of the series; "E," the Woods Hole example, closely resembled "F" (Fig. 4), the last of the primary group. The "head" is now broad anteriorly, but does not as yet approach the rounded form characteristic of the "head" of the adult *P. filosa*. In "E" the antennæ were nearer the anterior margin of the "head" than was the case with "D," but were not visible from below. A trace of the cephalothoracic border is still present in this anterior dorsal region. The rostrum has disappeared and the venter of the anterior part of the "head" is covered with small tubercles, amid which the tubercles already introduced are lost. In specimen "E" the median one of the older series could just be identified. This specimen also exhibited faint traces of the median eye and the condition of its abdominal appendages was similar to that existing in "D," the six anterior pairs being unbranched, the remaining pairs having a longer outer and a shorter inner ramus. The rami are longer than the rami of "D's" appendages, however. All the abdominal appendages of "F" on the other hand had two

accessory branches and so further approached the complexly-parted appendages of the adult. The dimensions of "E" were; head 3 mm., thorax 150 mm., abdomen 9 mm. The head was 2 mm. wide and the horns spread 3.5 mm. The total length of "F" was 133 mm.

Although fundamentally similar, in several points the development shown by this series differs from the only previous description of undoubted *Penella* larvæ which I have been able to find, that recorded for *P. varians* by Steenstrup and Lütken ('61). This earlier account starts with a larva (Fig. 5) unquestionably much more immature than the youngest form in my series.

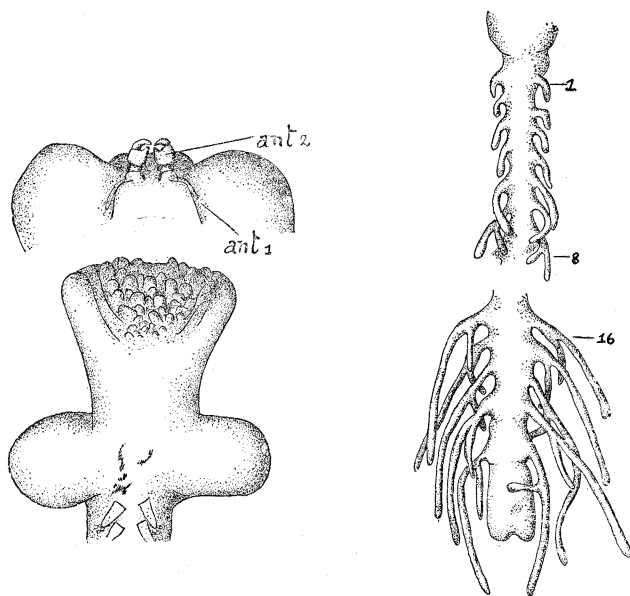


FIG. 4. Head of most mature larva of *P. filosa*; "F". Anterior and posterior extremities of the abdomen of larva "E".

This individual seems to have been about one centimeter in length, was filiform with a highly-convex cephalothorax, succeeded by three short thoracic segments, a long thoracic segment and a short, segmented(?) abdomen. This latter region lacked lateral appendages. The relative proportions of cephalothorax, thorax, and abdomen were — as shown in the figures — about 1' 4' 1' ;

the posterior or "genital" thoracic segment being ten times as long as the three anterior rings together. The length of the thorax here shown proportionate to the cephalothorax and abdomen is in marked contrast to the excessively elongate thorax of the *P. filosa* larva "A," where the relative lengths of the three body regions are as 1' 32' 5'. However, the unlikeness should not be wholly referred to the difference in the ages of the two specimens, because in fully-mature specimens of *P. varians* the

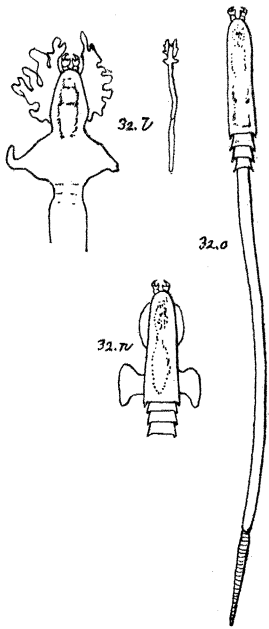


FIG. 5. Youngest, and second and fourth oldest larva of *P. varians*. (From Steenstrup and Lütken.)

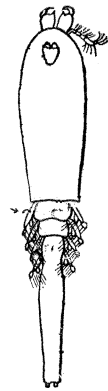


FIG. 6. *Baculus elongatus*. (From Lubbock.)

thorax is proportionally much shorter than with *P. filosa*. The older larvæ of *P. varians* figured by the Danish observers show a gradual approach toward the proportions characteristic of the adult — 1' 7' 2' as figured — although the abdomen remains in all disproportionately long. On the other hand, in the *P. filosa* series the thorax is about twice as long proportionally to the "head" and abdomen as in the adult; these regions only attaining their final dimensional relations later in the course of the development.

As with *P. filosa*, the horns of *P. varians* develop as a pair of outgrowths from the sides of the posterior part of the cephalothorax. The metamorphosis of the anterior part of this region of the body to form the "head" is also fundamentally similar in both species. In detail, the development shows noticeable differences. With *P. filosa* no division of the thorax into segments is traceable in my youngest larva, although this has no horns or "head." Later; the sides of the anterior cephalothorax become inflated, early destroying the convexity and distinct borders of the region. The mouthparts are gradually replaced by tubercles, the first of which to appear arise in a definite order. With *P. varians* (Fig. 5) the sides of the anterior region of the cephalothorax beneath the lateral borders of the shield early form two rounded outgrowths, while nearer the posterior end of this part of the body the horns protrude as two longer, pointed outgrowths. This occurs before the separate thoracic segments lose their identity and while the cephalothoracic shield is still distinct in all parts. In an older specimen of this species, the anterior or "head" outgrowths are shown to be broadened and have fimbriated margins. At this time the boundaries between the cephalothorax and thorax and those for the individual thoracic segments are no longer distinguishable while the borders of the cephalothoracic shield are still recognizable anteriorly and the mouthparts are intact. The later metamorphosis is not known.

The rostrum, mouthparts and antennæ of the *P. varians* larvæ seem to have been very like those described for my larvæ. The thoracic limbs are figured with the two anterior pairs bi-ramous, the two posterior pairs uni-ramous. No account is given of the changes which the cephalothoracic appendages undergo, nor of the development of the lateral appendages of the abdomen. It is clear that the latter were not present in any of the larvæ described and the implication is that their development is markedly retarded, although no definite statement is made with regard to this point. It is not improbable that in this species the adult shape of body and "head" may be attained before the abdominal appendages are developed. Such would appear to be the case with another species of *Penella* at least, *P. exocæti*, for Steenstrup and Lütken ('61) figure specimens which have a "head" of

almost adult form but lack abdominal appendages. The sexually mature *P. exocæti* evidently possesses abdominal appendages that are subdivided into several branches. The relative development of abdominal appendages compared with the "head" in the oldest specimen of the *P. filosa* series — "F" — suggests the possibility of a somewhat similar phenomenon here, to the extent that individuals may occur with the general appearance of an adult, but with less complexly cleft appendages. Such approaches in development to an adult bodily form before the abdominal structures have fully shaped themselves deserve notice, if only from the standpoint of the systematist. They may readily become not unimportant sources of confusion.

Moreover with *P. varians* the abdominal appendages are variable even in the adult animal, Steenstrup and Lütken recording them as bifid for several mature individuals (p. 411) although they are typically uniramous. With *P. filosa* the abdominal appendages of all the specimens of mature form that I have had opportunity to examine, were complexly subdivided into filamentous branches. The occasional presence of one or more simple or few-parted appendages at the anterior end of the series was the only variation found. This occurred in two out of seventy-nine specimens from *Orthogoriscus mola* in a collection loaned me by the Museum of Comparative Zoölogy. At least one of these was sexually mature and bearing egg-sacs and the same was true for a single specimen out of fifteen examples from the swordfish, which individual had three of the anteriormost abdominal appendages tri-ramous only. The number of the abdominal appendages is fairly constant in *Penella filosa*; varying from 21 to 30 pairs. Twenty-two or twenty-five pairs are the commonest. Of my larvæ: "A" had 22 pairs, "B" 21, "C" 23, "D" 21, "E" 20 and "F" 22.

On comparing the youngest *Penella* larva known, the immature *P. varians* figured by Steenstrup and Lütken, with that stage of the ontogeny of *Lernæa branchialis* at which fertilization and attachment to the final host takes place — the "begattungsstadium" of Claus' ('68) description — or to the corresponding phases of other lernæoid copepoda, the resemblance in general structure is striking. And it appears probable, therefore, that

the larva of *Penella* at the time when it attaches to the host has a form not unlike this "mating-stage" of the *Lernæa*. That is, it will closely resemble the youngest stage of the *Penella varians* series with the exception that the posterior or genital segment of the thorax will not be as disproportionately long in comparison to the rest of the body. Very probably this segment will not be sharply distinguished from the abdomen, as in the case in *Lernæa* of this age. A number of years ago Wierzejski ('77) described certain larval Copepods from the gills of *Loligo*, *Sepia* and *Eledone* at Triest and suggested that they might be the mating-stage and younger larvæ of *Penella varians*. His opinion was based on the characters exhibited by the appendages. As figured, however, these structures do not appear to be at all conclusive with regard to this hypothesis and in general form the larvæ certainly do not at all correspond to what would be inferred for the mating-stage of any *Penella*. Two minute immature Copepods have been recorded which seem to fill the requirements better. These were described under the names *Baculus elongatus* (Lubbock, '60) and *Hessella cylindrica* (Brady, '83). The former was collected in the Gulf of Guinea, the latter off Zamboanga in the Sulu Archipelago. Although not wholly alike in all structural details, they agree in possession of a filiform shape, cylindrical cephalothorax with projecting second antennæ, short segmented thorax, with four pairs of limbs, and an elongate hind-body devoid of lateral appendages and evidently representing a fusion of the posterior part of the thorax with the abdomen. Lütken in 1892 strongly urged that *Baculus elongatus* be regarded as a larva of *Penella*. He points out that *Baculus elongatus* is a pelagic form, in harmony with the fact that the genus *Penella* infests "fishes or whales with a more or less marked pelagic habit (*Xiphias*, *Coryphæna*, *Exocætus*, *Diodon*, *Mola*, *Pterophryne*, *Hyperoödon*, *Bulænoptera*).". The filiform shape of these larvæ unquestionably suggests *Penella* and the argument from habitat is significant. But, nevertheless, it must be admitted that on a basis of present knowledge of the forms a definite determination is not possible. We can only say that *Baculus* or *Hessella* are almost certainly the young of lernæoid copepods, possibly of *Penellas*. However this may be,

these larvæ are helpful in constructing a picture of the hypothetical mating-stage phase of *Penella's* metamorphosis.

Attached to the host while possessing such a *Baculus*-like form, probably at first by the antennæ, then later burrowing into the tissues, the retrogressive metamorphosis begins. An elongation of the posterior thoracic segment brings about a condition in which the young *Penella* will parallel the earliest described stage of *P. varians*. Then the adult form is gradually developed. The anterior part of the cephalothorax moulds itself into the "head," the horns protrude from the posterior part of this region, the thoracic segments coalesce, the anterior ones remaining undeveloped, the posterior elongating to form the major part of the body, while the abdomen develops the characteristic lateral appendages.

As regards the metamorphosis prior to the attainment of the mating-stage form, we only know that the young *Penellas* almost unquestionably hatch as nauplii. The analogies presented by the development of *Lernæa* and allied copepods (Scott, '01, Claus, '68) suggests the following cycle in the period between the nauplius and the completed, fertilized, mating-stage larva. The nauplius probably metamorphoses to a cyclops-like form, the so-called "*Chalimus*" stage, and in this phase the young attach themselves to some host. Typically among parasitic copepods, the attachment in this chalimus stage is made by a frontal filament. While thus fixed on the host, the mating stage is reached by successive moults. At this point in the ontogeny of *Lernæa* the male and females copulate and the latter detach themselves and for a short period return to a pelagic life. Then they settle down upon the final host, which happens to be a different kind of fish from the one they infested during the earlier part of their life. Other parasitic copepods pass through a similar life cycle on a single species of animal as host. Of course we have no clue to which of these groups *Penella* belongs, but its Lernæonoid affinities suggest a metamorphosis with the double host. Nevertheless, this possibility should in no way discourage the most careful scrutiny of freshly captured fishes that are infested with *Penellas* or are species which serve as hosts for this genus, if opportunities present themselves. The metamorphosis

must run a course similar to that in *Lernæa*, and if only a newly-attached mating-stage larva could be identified and described, it would go far toward the unravelling of the life-history of these highly-modified copepods.

Similarly, the discovery of the males for this genus is much to be desired. Steenstrup and Lütken ('61) record finding near the egg-sacs of a *Penella exocæti* two almost microscopic animals which reminded them of the "pigmy males of other lernæan forms." They figure one of these with the suggestion that it may be the vainly sought male. The specimens could not be removed for study. It is very doubtful whether this is a male of *Penella*. It would seem that the male of this genus ought rather to resemble the male of *Lernæa* and its form will be cyclopoid much like that of the chalimus stage of the females. As with *Lernæa* also, it is unlikely that the males remain attached to the females after fertilization has taken place, but continue on the host which has served them for their earlier development, while the females become free swimming after fertilization and settle down on another animal of the same or another species from the first host.

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